A Review of the Scientific Literature on Fungus Gnats (Diptera: Sciaridae) in the Genus *Bradysia*[1, 2]

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J. Entomol. Sci. 31(3): 252-276 (July 1996)

ABSTRACT The majority of the literature concerning fungus gnats in the genus *Bradysia* (Family Sciaridae) can be divided into two groups, addressing their cytogenetics or their role as economically important pests. Cytological anomalies in sciarids are recognized in (1) chromosome complement, (2) differential chromosome contributions of the sperm and egg, (3) alteration of chromosome complement during embryogenesis, (4) and alteration during gametogenesis. The literature concerning these cytological events is reviewed within the context of the development of the science of cytogenetics and as they relate to the taxonomy and systematics of this group. Although species of *Bradysia* were recognized as pests of various seedling plants over a century ago, their economic importance in plant and mushroom production was largely overlooked until recently. A review of the scientific literature on the biology and management of the sciarids indicates that members of the genus *Bradysia* may be especially pestiferous in greenhouse plant production. Although, a fungal food source appears to be critical to successful development and reproduction of fungus gnats, larvae also will feed on healthy plant tissue. Feeding activities of larvae directly damage seedlings, whereas both larvae and adults indirectly contribute to plant damage through the spread of fungal phytopathogens. The relatively recent confirmation of fungus gnats as potential disseminators of plant pathogens has placed these insects in the category of a more serious pest. As expected with any recently recognized pest, critical information regarding monitoring and economic thresholds is lacking. However, because these flies have been considered a nuisance, chemical control methods are available, as are alternatives which have been integrated most successfully into management programs in European glasshouses.

KEY WORDS Fungus gnats, sciarids, literature review, chromosome elimination, *Bradysi*

Fungus gnats in the genus *Bradysia* (Diptera: Sciaridae) are true flies commonly referred to as the darkwinged fungus gnats. These insects inhabit moist shady areas within woodlands, greenhouses, mushroom cellars, and field crops (Beling 1886, Hungerford 1916, Thomas 1931, Springer and Carlton 1993). The adults are small (average length of males is 2.5 mm, females 3 mm) and inconspicuous, frequenting the area between the soil surface and lower foliage

[1] Received 09 June 1995; Accepted for publication 25 April 1996.

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(Chittenden 1901, Wilkinson and Daugherty 1970, Kennedy 1976). Fungus gnats are weak flyers, but very active and rapid runners (Hungerford 1916). One species in particular was given its common name, the fickle midge, due to its unusual running behavior as first noted by Fitch (1856). Chittenden (1901) describes this behavior as "advancing two or three inches and then abruptly pausing or moving backward a step or two and instantly running in another direction."

Fungus gnats are common insects in greenhouses where for many years they were considered merely a nuisance. However, direct damage to plant roots and commercial mushrooms caused by fungus gnat larvae, along with a recognition of the role these insects may play in pathogen dissemination, has elevated them to pest status. No one recently has reviewed available information for these pests (Hungerford 1916, Thomas 1931, Steffan 1966). Therefore, our purpose herein was to provide a current review of literature on fungus gnats in the genus *Bradysia*.

Cytogenetics and Sex Determination

The giant chromosomes found within the salivary glands of some larval dipterans provided much of the experimental material for the development of cytogenetics as a scientific field (White 1954). Species within three families-Chironomidae, Drosophilidae, and Sciaridae-were most intensively studied as members of all three possess salivary gland chromosomes that are particularly favorable for detailed analysis (White 1949). Despite substantial early interest in species of *Bradysia,* additional characteristics facilitating genetic investigation have resulted in *Drosophila* becoming one of the most heavily studied animal genera.

Drosophila are easily cultured and have a significantly shorter lifecycle than fungus gnats-1 week in comparison with 2 to 3 weeks (Hungerford 1916, Wilkinson and Daughtery 1970, Kennedy 1974). However, the most important factor leading to the greater volume of genetic experimentation on *Drosophila* was the ease of obtaining phenotypically-expressed genetic mutations. In comparison, obtaining mutant characters in *Bradysia* was considered difficult (Smith-Stocking 1936). The spontaneous or naturally-occurring mutation rate of *Drosophila* is high, whereas that of *Bradysia* is low (Metz 1938a). Similarly, inducing mutations in *Drosophila* was relatively easy in comparison with *Bradysia*. The mutagenic action of X-rays was first demonstrated by Muller (1927), work for which he was awarded the Nobel Prize. Kimura (1983) describes Muller's special purpose stocks as making "*Drosophila* the unrivalled experimental organism for genetical studies." Using X-rays to induce mutations yields ten times as many mutants in *Drosophila* as in *Bradysia* (Metz 1934). Metz (1934) postulated viscosity characteristics of the chromosome matrix in Sciara provide the chromosomes a high level of stability even under X-ray bombardment. Improved experimental techniques did little to remedy the scarcity of mutant characters in *Bradysia*. More recently, Crouse (1960a) indicated that genetic studies of *Bradysia* had been handicapped by the dearth of genetic markers, limited to one mutant per autosome and two sex-linked mutants.

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The number of cytogenetic studies using *Bradysia* may not have kept pace with those of *Drosophila* as a result of the researchers involved and the times in which they respectively worked. Charles Metz was one of the pioneers in the early 1900's of the study of dipteran cytology (1914, 1916a, 1916b). Through careful experimentation he and his colleagues unraveled the cytological mechanisms of sex determination among sciarids (Metz 1925, 1928a, 1929a, Metz and Ullian 1929, Metz and Schmuck 1931, Schmuck and Metz 1932, DuBois 1932, Berry 1941, Crouse 1960b). Metz concentrated his efforts on cytological analyses and seldom offered an interpretation of the adaptive significance of the genetic anomalies that he described. In contrast, Theodoseus Dobzhansky was one of the leaders in research which combined cytology and genetics, providing an early synthesis of modern evolutionary thought in *Genetics and the Origin of Species* (1937). His studies of inversion polymorphisms using the salivary gland chromosomes of *Drosophila* were initiated during the 1930's (Dobzhansky and Tan 1936a, 1936b, Dobzhansky and Sturtevant 1938). Dobzhansky used recognizable inversions in species of Drosophila to develop many of his hypotheses of genetic change as related to evolution (Dobzhansky 1937, 1941, 1951, 1970).

Despite the focus on *Drosophila*, the atypical segregation and elimination of chromosomes among several sciarid genera have been well characterized. These cytological anomalies Metz and others investigated in the Sciaridae are highly interrelated and best understood when contrasted to the more typical events of mitosis and meiosis. The following is intended as a brief summary of these events and in part follows an outline given by Metz (1938b). Cytological deviations in sciarids are recognized in the (1) chromosome complement, (2) chromosome contributions of the sperm and egg, (3) alteration of chromosome complement during embryogenesis, and (4) alteration during gametogenesis.

Typically, the chromosome complement of an individual organism consists of a constant number of autosomes and sex chromosomes, diploid in the soma and haploid in the gametes. Species of *Bradysia*, however, possess an additional type of chromosome which is limited to the germ-line. These structures, therefore, have been referred to as "limited" chromosomes (Metz 1938b).

The second cytological anomaly observed among species of *Bradysia* is a difference in chromosome contributions of the sperm and egg. Both egg and sperm contribute a species specific number of limited chromosomes (McCarthy 1945). In addition, the egg contributes a typical haploid chromosome complement consisting of three autosomes and a single sex chromosome (X or X^1). The sperm, however, contains a haploid set of the three autosomes plus two copies of the X chromosome. Therefore, each zygote begins development with a varying number of limited chromosomes, three pairs of autosomes and three X chromosomes, two of which were contributed by the sperm. Moses and Metz (1928) established that fertilization is monospermic, thereby eliminating speculation that the extra sex chromosome resulted from fertilization by multiple sperm.

The initial chromosome complement of the zygote is altered during the course of several early cleavage divisions. At the fifth or sixth cleavage, a distinction occurs between cells destined to become somatic tissue from those of the germ line. At this time any limited chromosomes are eliminated from future

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somatic cells during mitosis. At the seventh or eighth cleavage of these cells elimination of one or two X chromosomes occurs. If one is eliminated, the somatic cells will be X^1X and the individual will develop as a female. If two are eliminated, the soma will be XO and result in development of a male.

The remaining anomalous cytological event observed among species of sciarids is the elimination of two X chromsomes during the first spermatocyte division. This is followed by an unequal division of the chromatoids resulting in both halves of the remaining X chromosome moving to one pole during meiosis. One spermatid is produced instead of the typical four from each primary spermatocyte, and only one type of sperm (XX) is produced in place of the expected two (X or O). The studies which determined the mechanisms of these unique chromosomal elimination events were as interrelated as the events themselves. The following is a chronological account of the investigations and associated results.

Metz (1928b) reported several species of sciarids to characteristically produce unisexual or monogenic offspring through pair matings, resulting in all male or female progeny. At this time, the production of unisexual progeny was recognized in other animal groups and attributed to parthenogenesis, gynogenesis or alternation of generations (Wilson 1925). None of these phenomena, however, were observed among species of sciarids. Sex determination in these insects first was believed to be controlled by the chromosome complement of the male. Metz (1928a) assumed the genetic mechansim in *B. coprophila* (Lintner) that enabled production of unisexual progenies to be the common XX-XY arrangement in which the male carries the XY complement and produces two sperm types. This assumption was supported by observation of pairing a single male with multiple females resulted in production of both male and female offspring, whereas the progeny of a single female were always of one sex (Metz and Ullian 1929). Metz (1929b) tentatively concluded that selective fertilization of the eggs of an individual female by one sperm type (X or Y) occurred and was dependent on the zygotic constitution of the female. Subsequent investigation by Metz and Schmuck (1931), however, suggested that males arise as the result of the elimination of sex-chromosomes during early cleavage divisions of embryogenesis.

DuBois (1932, 1933) confirmed this suggested scheme of sex determination when she established sex-chromosome elimination to occur at the seventh cleavage in the somatic nuclei. This event establishes the earliest differential between female and male embryos. Thus, the somatic cells of males contain seven chromsomes (a single sex chromosome and three pairs of autosomes), whereas those of females contain eight (a pair of sex chromosomes plus three pairs of autosomes).

Metz (1934) later determined that males did not possess an X and a Y chromosome, but instead possessed a single X chromosome (XO). The first event leading to this condition is selective elimination of the paternally derived X chromosome at the first meiotic division in spermatogenesis (Berry 1941). At the second meiotic division the remaining maternally derived X chromsome divides and undergoes equational nondisjunction resulting in both copies moving into the sperm nucleus. Thus, fertilized eggs begin with three X chromsomes, two paternally and one maternally derived, in addition to three pairs of equably derived autosomes.

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These elimination events are possible only as the result of cellular differentiation of sex chromsomes from autosomes and recognition of their derivation (maternal or paternal). The search for recognition mechanisms lead to additional cytological studies. Using a series of rare reciprocal translocations between the sex chromosome and autosomes, Crouse (1960b) was able to demonstrate in *B. coprophila* that the terminal mass of heterochromatin on the sex chromosome and not the entire chromosome, is recognized during spermatogenesis and embryogenesis. Similarly, limited chromosomes are very dense and heterochromatic (Metz 1938b) and their heterochromatic structure may provide a recognition factor for selective elimination from the presumptive soma during embryogenesis, although this has not been examined. Perondini et al. (1986) have shown that compartmentalization during early embroyonic development allows somatic and germ line nuclei to be exposed to different signals. Similarly, chromosome elimination in germ line nuclei is facilitated by the presence of distinct maternal and paternal nuclear compartments occupied by the respective haploid chromosome sets in a consistent orientation along a cellular axis (Kubai 1987).

Although the mechanisms responsible for the anomalous events of spermatogenesis and embryogenesis among some species of *Bradysia* have been elucidated, the adaptive significance, if such exists, has not been made clear. Metz (1938b) has suggested the production of unisexual progeny could be a means of insuring outcrossing. The cytological investigations have significantly contributed to inferring systematic relationships in the Sciaridae (Steffan 1966).

Taxonomy and Systematics

Winnertz (1867) recognized Sciaridae as a distinct family and proposed four new genera – *Trichosia, Cratyna, Corynoptera and Bradysia* – following the study of European specimens. Johannsen (1912) developed the first extensive taxonomic key for North American species placing them in the Sciarinae, however, a subfamily of Mycetophilidae. Taxonomists had grouped sciarids and mycetophilids together based entirely on morphological similarities. Using cytological analysis, White (1949) divided the suborder Nematocera into four groups placing the families Sciaridae and Cecidomyidae by themselves based on their highly anomalous chromosome cycles. The genera in the Family Sciaridae were revised by Steffan (1966) who placed several species, which had formerly been recognized as species of *Sciara,* in the genus *Bradysia*.

Among sciarid genera, *Bradysia* contains the greatest number of species in either north America or Europe. According to Steffan (1966), there are approximately 150 species in the family Sciaridae in North America, 65 of which are in the genus *Bradysia*. In New York alone, 35 species of sciarids occur, 20 of which are in the genus *Bradysia* (Johannsen 1912, Shaw and Fisher 1952, Wheeler 1971). The genus, as a whole, is distributed worldwide.

Steffan (1966) gives the following combination of morphological characters to distinguish the genus *Bradysia* from other North America genera: "maxillary palpi three-segmented, usually with sensory pit, protibiae with preapical, ventral, unilateral comb separated from general tibial vestiture by triangular bare area, metatibiae with two subequal spurs, and posterior wing veins bare."

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Cytological analyses also provide insight into the systematics of this group. Boyes (1958) suggested the ancestral chromosome complement in this genus to have been 4 metacentric (V-shaped) pairs. If this hypothesis is accepted, then the species and strains of *Bradysia* which possess 2 metacentric and 2 acrocentric (rod shaped) chromosomes (2V/2R) appear to be ancestral to the species and strains that possess 1 metacentric and 3 acrocentric chromosomes (1V/3R) (Table 1). This also would suggest that monogeny is derived and digeny is the ancestral trait, as monogenous speices and strains of *Bradysia* possess a 1V/3R complement, whereas digenic *Bradysia* are 2V/2R. This hypothesis is further supported by the chromosome complement of speices in the closely-related genus *Lycoriella*. Taking this genus as an outgroup, the chromosome complement 2V/2R of *L. agaria* (Felt), *L. fenestralis* (Zetterstedt), *L. mali* (Fitch), and *L. multiseta* (Felt), all species that exhibit digeny, again supports monogeny as the derived character. The exception is *L. similans* (Johannsen) which produces a pure monogenic strain, yet possesses the 2V/2R chromosome complement associated with digeny in *Bradysia*.

The number and type of limited chromosomes can be considered in a similar manner. Limited chromosomes fragment easily and appear to contain relatively few genes. From an evolutionary standpoint Metz (1938b) suggested limited chromosomes as being in the process of disappearing. McCarthy (1945) offered the metacentric type to be the ancestral form of these chromosomes. If these hypotheses are accepted, then acrocentric limited chromosomes should be considered derived and the lack of any limited chromosome to be the more recently derived condition (Table 1). The suggested lines of evolutionary change that have occurred among the limited chromosomes, however, do not parallel those discussed for the autosomes and, thus, cannot be used to support monogeny as derived. Furthermore, limited chromosomes are eliminated from the somatic cells and thus from the salivary gland chromosomes, consequently, their structure has not been studied as well as that of the other chromosomes.

Analysis of yet another type of chromosomal change-inversions-may be used to generate a phylogenetic history within a species of *Bradysia*. Dobzhansky and Sturtevant (1938) constructed such a phylogenetic tree for a species of *Drosophila* by determining the order in which overlapping inversions must have occurred. Similarly, *B. impatiens* (Johannsen) has been described to contain numerous long inversions (Carson 1944). These inversions do not overlap; however, the order in which the changes occurred can be reconstructed by analyzing the gene deficiencies often associated with either end of an inversion. Carson used deficiency analysis to develop unidirectional phylogenies for several gene arrangements on the chromosomes of *B. impatiens*.

Inversions have been observed in five of six species of *Bradysia* examined cytologically (Table 1) and, when first detected in *D. melanogaster*, were considered suppressors of crossing-over (Morgan 1911). Dobzhansky and Epling (1944) and Carson (1944) point out that the great number of inversions give rise to polymorphisms within fly populations. Dobzhansky (1970) adds that "this is probably not accidental" given the absence of synapsis in male meiosis. It has been suggested that in the absence of crossing over, a chromosome can accrue mutations which may provide an isolating mechanism for speciation (Carson 1944). A possible example may be observed by comparing the C-autosome of

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Table 1. Summary of progeny production type and chromosome characteristics for species studied cytogenetically in the Sciaridae (after Steffan 1966).

Valid name (Steffan 1966)	Name used in literature	Progeny type	Chromosome complement	No. limited chromosomes	Observed inversions	Scource
Lycoreilla mali	*Sciara pauciseta* and *S. fenestralis*	digenic* (monogenic)	2V / 2 R	2V	√	McCarthy (1945)
L. fenestralis	*S. fenestralis* Form II	monogenic* (digenic)	2 V / 2 R	1V	√	McCarthy (1945)
L. agaria	*S. agaria*	digenic	2 V / 2 R	1V		McCarthy (1945)
L. multiseta	*L. multiseta*	digenic	2 V / 2 R	1V		Steffan (1966)
L. similans	*S. similans*	digenic strain	2 V / 2 R	1V		Metz (1926)
		monogenic strain	2 V / 2 R	1V		
Bradysia prolifica	*S. prolifica*	digenic	2 V / 2 R	1V	√	McCarthy (1945)
B. reynoldsi	*S. reynoldsi*	digenic	2 V / 2 R	0	√	Crouse (1939)
B. tritici	*S. ocellaris*	digenic strain	2 V / 2 R	0	√	Crouse (1939)
		monogenic strain	1 V / 3 R	0	√	
B. coprophila	*S. coprophila*	monogenic	1 V / 3 R	1 to 2 V		Metz (1931)
B. impatiens	*S. impatiens*	monogenic	1 V / 3 R	1 V	√	Carson (1946)
B. sp VII	*S.* sp. VII	monogenic	1 V / 3 R	2 R	√	Crouse (1939)
Scatopsciara sp. XXIII	*S.* sp. XXIII	digenic	4 R	2 R		McCarthy (1945)
S. nacta	*S. nacta*	digenic	4 R	2 R	√	McCarthy (1945)
S. sp XXV	*S.* sp. XXV	digenic	1 V / 3 R	0		McCarthy (1945)

* Predominantly of the progeny type listed although some production of the parenthetical type.

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B. reynoldsi (Metz) to that of *B. tritici* (Coquillett), the only two species known to produce viable hybrids (Metz and Lawrence 1938). These closely-related species share a triplet repeat on the X-chromosome, but differ by two inversions in the C-autosome (Crouse 1939). Such a potential isolating mechanism has not been investigated in relation to the process of speciation in the genus *Bradysia*.

Although there has been limited speculation as to the phylogenetic relationships among species of *Bradysia*, these relationships have not been investigated (McCarthy 1945, Boyes 1958, Steffan 1966). Molecular techniques developed since these cytogenetic studies were conducted could clarify such relationships and establish the ancestral and derived states of chromosome shape and number, as well as that of monogeny versus digeny.

Life History

Males of *Bradysia* spp. generally emerge 1 d prior to females; an approximate 24-h preoviposition period follows female emergence during which mating occurs. Genetic studies indicate that females are inseminated by only one male (Crouse 1943). Adults are short-lived (approximately 3 d), males usually living longer than females which die soon after oviposition (Steffan 1966, Kennedy 1976).

Male and female fungus gnats in the genus *Bradysia* exhibit distinctly different mating behaviors. Females are less active, and therefore less conspicuous than males and can be found standing on the underside of leaves or on vertical surfaces near the soil surface (MAH, pers. observation). Females produce a pheromone which elicits wing fanning and zig zag running by males (Alberts et al. 1981). Males approach the slightly larger females while fanning their wings and simultaneously curling their abdomens forward underneath the thorax in a manner similar to that described by MacDonald (1972) and Kostelc (1977) for *L. mali*, a closely-related sciarid pest of mushroom production. Recognition of these behavioral differences can greatly facilitate establishment of laboratory cultures from field-collected individuals.

Species of *Bradysia* are multivoltine, the number of eggs deposited per female by female-producing *B. impatiens* averages 111, whereas male-producing females deposit an average of 153 eggs (Carson 1945). Similarly, overall fecundity of female *B. impatiens* are reported as averaging 150 (Carson 1945), 142 (Kennedy 1974), and 100 eggs (Perondini et al. 1986), whereas Wilkinson and Daugherty (1970) observed an average of only 75 eggs per female. Thomas (1931) dissected 272 eggs from a single female *B. coprophila*. The average length and width of the oblong *B. impatiens* egg is 189 μ and 98 μ respectively (Carson 1945). Sperm are stored in a spermatheca and eggs fertilized singly upon oviposition (Crouse 1943). Fertilization has been determined to be monospermic (Moses and Metz 1928).

The egg stage is followed by four larval instars and an obtect pupa. The presence of a shiny black head capsule on an otherwise translucent or white vermiform body distinguishes fungus gnat larvae from other immature dipterans. An exhaustive study of the morphology of the first larval instar of *B. tritici* reveals sufficient cuticular detail to distinguish individual segments (Bischof et al. 1985). Twelve denticle belts observed on the ventral side of the

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larvae are assumed by the authors to demarcate segment borders. The three thoracic segments may be differentiated by specific denticle patterns within these belts. Dorsal and ventrolateral sensillae patterns in combination with mechanoreceptor positions in relation to the denticle belts allow further identification of individual segments. Thus, developmental fate of embryonic cells can be determined through comparisons of experimentally altered cuticular patterns with recognized patterns, facilitating study of developmental signal translation during embryogenesis.

Both inter- and intraspecific variation in developmental times among *Bradysia* spp. has been reported. Development from egg to adult in *B. impatiens* has been measured in three studies at three different temperatures. Steffan (1966) observed an average developmental time of 16.3 days at 20°C, Wilkinson and Daugherty (1970) 19.9 days at 23.9°, and Kennedy (1974) 15 days for males and 16 days for females at 25° (Table 2). Similar variation in overall developmental time of *B. coprophila* has been reported: 24 to 32 days at an unknown temperature (Hungerford 1916), 18 to 23 days at 18°C (Thomas 1931), and 27 to 33 days at 23°C (Smith-Stocking 1936). This variation may reflect differing geographic isolates, food source, temperature, photoperiod, or experimental method (Kennedy 1971, Steffan 1974, Wessel 1989). The majority of variation in developmental time occurs during the larval stages as the egg and pupal stages are more consistent in duration. Individual larvae from the same cohort, however, may have highly variable developmental times when reared on the same diet (Hungerford 1916, Hellqvist 1994, MAH pers. obs.).

Kennedy (1976) describes fungus gnat adults as generally aphagous, however, they have been reported elsewhere as feeding on nectar (Mercier 1911), a sodium arsenate and molasses solution (Hungerford 1916), and "organic ooze" (Steffan 1966). Larvae primarily feed on fungi (Mercier 1911, Thomas 1931, Kennedy 1974, Anas and Reeleder 1988, Gardiner et al. 1990, Harris 1995) and can be cannibalistic (Steffan 1966, Wilkinson and Daughtery 1970, Harris et al. 1995). Fungus gnat larvae, although capable of feeding on healthy plant tissue, appear to do so only in the absence of a fungal food source. Kennedy (1974) observed *B. impatiens* larval survival to be reduced when fungal abundance was low which, in turn, resulted in reduced root damage. Survivorship and development of *B. impatiens* larvae on fungal and non-fungal diets also were investigated. He found that larvae developed more rapidly and exhibited greater survivorship on a diet which included a fungus. There appears to be a qualitative difference, however, among fungi in the diet of fungus gnat larvae. Anas and Reeleder (1988) observed that *B. coprophila* larvae failed to survive on fungus-free plant tissue, whereas larvae placed on plants inoculated with *Botrytis porri* Buckw., *Rhizoctonia solani* Kühn, or *Sclerotinia minor* Jagger exhibited high survivorship. In the same study, larvae placed on cultures of these fungi developed to adults that were able to successfully reproduce; whereas, larvae placed on cultures of the fungus *Trichoderma viride* Pers., a fungal antagonist, had very poor survivorship and no subsequent reproduction.

The effect of reduced availability of fungi in the diet of fungus gnats could provide a management tool for this pest. Fungal growth can be greatly reduced through the use of sterilized potting media in commercial plant production. Reduced fungal abundance could, in turn, reduce fungus gnat larval survival.

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Table 2. Number of days required for development of each life stage of *B. impatiens*, *B. coprophila*, and *B. tritici*.

Stage	*B. impatiens*			*B. coprophila*			*B. tritici*	
	23.9°C	25° (±1)	20° (±2)	–	~18°	23° (±1)	20° (±2)	
							monogenic	digenic
Egg	4	3.5	3.5	6	4-6	5.5	3	4.4
1st larval	3.3	2						
2nd Larval	3.1	2						
3rd Larval	1.8	2	9.6†	12-14†	14.2†	14.5†	12.2†	14.2†
4th Larval	5.9	3						
Pupa	2.4	3	3.9	6	3.6	3.5	3.3	3.6
Adult	6	–	–	7	–	–	–	–
Egg-adult	19.9	15m* 16f**	16.3	24-32	18-23	27-33	18.5	22.2
Reference	Wilkinson and Daugherty 1970	Kennedy 1974	Steffan 1974	Hungerford 1916	Thomas 1931	Smith-Stocking 1936	Steffan 1974	

* male
** female
† Combined larval stages.

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Furthermore, if a beneficial fungus such as *T. viride* were first established, larval survival could be further reduced (Harris 1995).

Rearing Methods

Various culture methods have been employed in the maintenance of laboratory colonies of fungus gnats. Hungerford (1916) reared *B. coprophila* on autoclaved potato by adding yeast and found dried blood fertilizer to be particularly attractive when added to a "breeding box". This box consisted of a potted plant fitted with a glass side to facilitate observation of feeding larvae. Hudson (1974) also found dried blood to be a useful addition to pots containing horse manure confined within muslin cages to rear *B. paupera* Tuomik. Manure has been utilized by various researchers to rear several species of fungus gnats, particularly *B. coprophila*, as its specific epithet might suggest (Thomas 1929, Austin and Pitcher 1936, Butt 1937).

Smith-Stocking (1936) established the agar culture method employed and modified by most subsequent researchers including Steffan (1966) and Kennedy (1973). Nonnutrient agar provides a consistently moist substrate on which eggs can be deposited and food consumed by larvae. Plastic containers with cotton pads and filter paper moistened with distilled water also can be utilized with the addition of a nutrient source such as ground soybeans (Wilkinson and Daughtery 1970). Another medium composed of moist peat and crushed kidney beans (Gillespie 1986) that supports fungal and bacterial growth was modified by Gardiner et al. (1990). Harris (1995) found the addition of lactic acid (0.1%) to the nonnutrient agar (2%) to be useful in reducing bacterial growth.

Economic Importance

Direct damage. In contrast to the generally aphagous adults, larval fungus gnats actively feed and can directly damage mushroom crops and the root systems of a variety of plants. As early as 1813, the destructive potential of larval fungus gnats was recognized in wheat seedlings and by 1901 in greenhouse plant production, particularly of cucumber (Olivier 1813, Chittenden 1901). Some of the same species also are reported as serious pests of commercial mushroom production (Thomas 1931). The list of plants which fungus gnat larvae have been observed to damage is extensive (Table 3). Although Hungerford (1916) reported feeding damage by fungus gnat larvae as being injurious to plants, the effects of such feeding on plant vigor remained unclear for many years.

Fungus gnat larvae attack the roots of many field-crop plants in addition to greenhouse-grown plants (Ellisor 1934, Metcalf et al. 1962, Fawzi and Kelly 1982). Soybeans damaged by larvae of *B. coprophila* reach maturity; however, these plants easily lodge and produce fewer seed than undamaged plants (Graham and McNeill 1972). Hamlen and Mead (1979) considered 5 to 10 larvae per pot-grown plant to represent a moderate infestation; however, such thresholds should be adjusted by plant age as seedlings appear to be particularly susceptible to damage (Coquillett 1895, Edwards and Williams 1916). Leath and Newton (1969) reported 90% of alfalfa seedlings killed at densities of less than

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Table 3. Crop plants reported attacked or damaged by fungus gnat larvae.

Floral Crop	Species Reported	Reference	Floral Crop	Species Reported	Reference
begonia	*Sciara inconstans**	Hungerford 1916,	lily	*S. inconstans*	McDaniel 1931,
	*S. caesar***	Weigel and Sasscer 1923,		*S. caesar*	Lindquiest et al. 1985
	S. prolifica†*	McDaniel 1931		*S. prolifica*	
				B. coprophila	
buttercup	*Sciara* sp.	McDaniel 1931	marigold	*B. impatiens*	Kennedy 1974
campanula	*B. tritici*	Kennedy 1971	nasturtium	*B. tritici*	Kennedy 1971
carnation	*S. inconstans*	Hine 1899,	orchard	*B. tritici*	Edwards and Williams 1917
	S. caesar	Weigel and Sasscer 1923,			Kennedy 1971
	S. prolifica	McDaniel 1931,			
	B. tritici	Kennedy 1971			
Christmas catus	*B. impatiens*	Hamlin and Mead 1979	peperomia	*B. impatiens*	Hamlen and Mead 1979
chrysanthemum	*S. inconstans*	Hungerford 1916,	pine	*B. impatiens Bradysia*	Kennedy and Helgesen
	S. caesar	MCDaniel 1931,		spp.	1973,
	S. prolifica	Lindquist et al. 1985			Keats et al. 1989
	B. coprophila				
cineraria	*S. inconstans*	McDaniel 1931	poinsettia	*B. coprophila Bradysia*	Lindquist et al. 1985,
	S. caesar			sp.	Nedstam and Burman 1990,
	S. prolifica				Harris et al. 1995
citrus	*S. inconstans*	McDaniel 1931	primrose	*S. inconstans*	McDaniel 1931
	S. caesar			*S. caesar*	
	S. prolifica			*S. prolifica*	
coleus	*S. inconstans*	Weigel and Sasscer 1923,	primula	*B. tritici*	Edwards and Williams 1916,
	S. caesar	McDaniel 1931		*Bradysia sp.*	Nedstam and Burman 1990,
	S. prolifica				Kennedy 1971
	Sciara sp.				

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Table 3. Continued.

Floral Crop	Species Reported	Reference	Floral Crop	Species Reported	Reference
croton	*S. inconstans* *S. caesar* *S. prolifica*	McDaniel 1931	rose	*S. inconstans* *Sciara sp.*	Chittenden 1901, McDaniel 1931
cyclamen	*Bradysia* sp.	Nedstam and Burman 1990	Saintpaulia	*Bradysia sp.*	Nedstam and Burman 1990
fern	*S. inconstans* *Sciara sp.s*	Weigel and Sasscer 1923, McDaniel 1931	smilax	*S. inconstans* *S. caesar* *S. prolifica*	McDaniel 1931
feverfew	*S. inconstans* *S. caesar* *S. prolifica*	McDaniel 1931	snapdragon	*S. inconstans* *S. caesar* *S. prolifica*	McDaniel 1931
foliage	*Sciara* spp. *Bradysia* sp.	Johannsen 1912, Hungerford 1916, Weigel and Sasscer 1923, Parr et al. 1954, Mead 1978, Hamlen and Wettstein 1978, Nedstam and Burman 1990	statice	*Sciara sp.*	McDaniel 1931
gerbera	*Bradysia* sp.	Nedstam and Burman 1990	stereospermum	*Bradysia sp.*	Nedstam and Burman 1990
geranium	*S. inconstans* *S. caesar* *S. prolifica* *B. tritici*	McDaniel 1931, Kennedy 1971	sweet alyssum	*S. inconstans* *S. caesar* *S. prolifica*	McDaniel 1931
gloxinia	*S. inconstans*	Chittenden 1901	sweet pea	*S. incosntans* *Sciara sp.*	Chittenden 1901, McDaniel 1931
iris	*Sciara* sp.	McDaniel 1931	tulip	*Sciara sp.* *S. inconstans*	Johansen 1912, Weigel and Sasscer 1923

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Table 3. Continued.

Floral Crop	Species Reported	Reference	Floral Crop	Species Reported	Reference
kalanchoe	*Bradysia* sp.	Nedstam and Burman 1990	verbena	*S. inconstans* *S. caesar* *S. prolifica*	McDaniel 1931
lupine	*Sciara* sp.	McDaniel 1931	violet	*S. inconstans* *S. caesar,* *S. prolifica*	McDaniel 1931
alfalfa	*Bradysia* spp. *B. impatiens*	Leath and Newton 1969, Kalb and Millar 1986, Springer and Carlton 1993	bean	*B. impatiens*	Hawley 1919, Kennedy 1974
asparagus	*S. inconstans* *S. caesar* *S. prolifica*	McDaniel 1931	carrot	*B. impatiens*	Hafidh and Kelly 1982
clover	*B. trifolii* *Bradysia* spp.	Petty 1918, Leath and Newton 1969	cucumber	*B. coprophila* *B. impatiens* *B. tritici* *Sciara inconstans* *Sciara sp.*	Chittenden 1901, Hart 1911, Speyer 1923, Kennedy 1971, Dennis 1978, Gardiner et al. 1990, Gillespie and Quiring 1990
corn	*Sciara* spp. *B. tritici*	Johannsen 1912, Kennedy 1971	lettuce	*Sciara inconstans* *B. tritici*	Chittenden 1901, Kennedy 1971
soybeans	*B. coprophila*	Wilkinson and Daugherty 1970, Graham and McNeil 1972	pea	*B. tritici*	Ellisor 1934, Chittenden 1901, Kennedy 1971

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Table 3. Continued.

Floral Crop	Species Reported	Reference	Floral Crop	Species Reported	Reference
tobacco		Fulton 1933	potato	*Sciara* sp. *B. tritici*	Hopkins 1895, Johannsen 1912, Gui 1933, MacLeod and Butcher 1934 Kennedy 1971
wheat	*Sciara* spp. *B. tritici*	Olivier 1813, Coquillett 1895, Johannsen 1912, Kennedy 1971	tomato	*Bradysia* sp.	Gillespie and Menzies 1993

* *Sciara inconstans* (Fitch), 1856 (*Molobrus*) species of uncertain position (Steffan 1966)
** *Lycoriella caesar* (Johannsen), 1923 (*Sciara*)
† *Bradysia prolifica* (Felt) (*Neosciara*)

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one *Bradysia* sp. larva per seedling. Springer and Carlton (1993) observed a higher ratio of seedling death to number of larvae and suggested that fungus gnats may reduce persistence of cool-season pasture legumes due to seedling mortality caused by feeding larvae.

We have observed a decline in *B. coprophila* numbers in Georgia greenhouses during the summer when temperatures are regularly above 32°C and an increase during the cooler months (maximum highs rarely exceed 26°C). Hawley (1919) noted a greater degree of plant damage by *B. coprophila* larvae of beans grown at a moderate soil temperature (24.4°C) compared to low (17°C) temperatures. Furthermore, plants grown at 32.7°C were uninjured indicating this temperature as being above the upper threshold. Wilkinson and Daughtery (1970) reported the lower and upper developmental thresholds for *B. impatiens* as 10 to 12.8°C and 32.2 to 35.0°C, respectively. This optimum temperature range predisposes these insects to infest crops grown in moderated environments such as greenhouses and mushroom cellars, where temperatures closely correspond to those commonly encountered in Georgia greenhouses except during the summer months.

Indirect damage. Fungus gnat larvae will feed on plant tissue that is free of fungal growth. When *Bradysia* sp. larval feeding in the absence of fungal root infection was observed, it was suggested by Leath and Newton (1969) that such feeding weakens plants, predisposing them to attack by pathogens. Graham and McNeill (1972) supported this suggestion with observations that soybean plants damaged by feeding *B. coprophila* larvae often appear to be infected by pathogens while undamaged plants remain healthy.

Fungus gnats have been observed in association with diseased plants for many years (Chittenden 1901). Mercier (1911) reported adult *Sciara thomae* L. drinking the sugary exudates of *Lolium perenne* L. infected with fungus *Claviceps purpurea* (Fr.) Tul., commonly known as ergot. Furthermore, he demonstrated that this insect was involved in the dissemination of *C. purpurea* not only by external contamination, but also in the insect's spore-containing "dejections." These findings appear to have been forgotten as subsequent literature continued speculation on the role, if any, fungus gnats play in pathogen dissemination.

In addition to disseminating fungal phytopathogens, contaminated fungus gnats can carry mycopathogens into mushroom production facilities. Charles and Popenoe (1928) noted fungal spores adhering to the legs and bodies of the adult fungus gnats. Several species in the genus *Lycoriella*, formerly identified along with *Bradysia* as *Sciara*, can cause tremendous loses in mushroom production by feeding damage and suspected introduction of pathogens (Thomas 1931, Wyatt and Binns 1977, Cantwell and Cantelo 1984).

Recent studies have elucidated the relationship of fungus gnats and several plant diseases. Kalb and Millar (1986) determined that adult *B. impatiens* were externally contaminated by spores of the fungus *Vetticillium albo-atrum* Reinke & Berthold and apparently dispersed this pathogen to healthy alfalfa plants. Fungus gnat larvae were frequently observed associated with diseased roots of seedlings in a conifer nursery by Keates et al. (1989) prompting the collection of adult fungus gnats to survey surface contaminants. Captured adults were found to be contaminated with numerous fungi including several identifiable

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pathogens such as *Botrytis cinerea* Pers. and species of *Fusarium*. Similarly, adult fungus gnats surface contaminated with *Fusarium oxysporum* Schlecht recently were demonstrated to successfully transport this pathogen to healthy bean and tomato plants (Gillespie and Menzies 1993). It has been suggested that fungus gnats also may spread *Pythium* in greenhouse crops (Favrin et al. 1988). Spores of *Pythium* spp. survive passage through the digestive tract of *B. impatiens* larvae not only retaining viability, but also germinating normally, implicating fungus gnat larvae in pathogen dissemination via excretion (Gardiner et al. 1990). Jarvis et al. (1993) demonstrated that *B. impatiens* larvae that ingest propagules of *P. aphanidermatum* (Edson) Fitzp. then are capable of introducing this pathogen to seedlings when feeding on the roots.

Another fungal pathogen often associated with infestations of both fungus gnats and shore flies, *Scatella stagnalis* (Fallen), is *Thielaviopsis basicola* (Berk. & Br.) Ferr. Infections by this phytopathogen cause a root rot which has been considered one of the more important diseases in production of such floricultural crops as poinsettia, *Euphorbia pulcherrima* Willd., and various bedding plants (Bateman 1961). Infections of bedding plants by *T. basicola* recently have resulted in significant economic losses that were particularly severe in pansy crops, *Viola* spp. hybrids (Barnes 1990).

Even though *T. basicola* is considered a root pathogen, it can produce substantial above-ground sporulation on infected plants increasing the possibility of contaminating visiting insects (Stanghellini and Rasmussen 1994). It is possible for adult fungus gnats to become contaminated with *T. basicola* spores. Harris (1995) demonstrated that both larvae and adults of *B. coprophila* can disseminate *T. basicola* to pansy seedlings by surface contamination, alimentary tract contamination, or by viable spores surviving passage through the alimentary tract.

There have been no controls developed for *T. basicola* other than use of conventional chemical fungicides. None of the fungal antagonists reported to date have been efficacious against this pathogen (Papavizas 1984). *Fusarium proliferatum* (T. Matsushima) Nirenberg, however, recently has been shown to be a potential antagonist of *T. basicola* and to be disseminated by *B. coprophila* larvae and adults (Harris 1995).

Monitoring Methods

Various methods have been utilized for monitoring numbers of fungus gnats. Rutherford et al. (1985) compared arrangement and quantities of white sticky traps placed in commercial cucumber greenhouses to monitor abundance and distribution of adults. In addition, soil cores were examined to determine the number of larvae per volume. The authors found that fewer traps placed in a "W" pattern closely correlated with a more intense, random placement of traps. No correlation was determined between the number of adults on traps with the number of larvae. Similarly, Harris et al. (1995) report no correlation between numbers of adults on yellow sticky traps with larvae associated with potato discs placed on the media surface of potted poinsettias. Larvae congregate underneath these discs and can be reliably used to indicate actual numbers of larvae in soil. Larval densities also have been determined by partially submerging potted

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plants in water forcing the larvae to concentrate in the upper centimeter of the soil. Larvae can then be collected and counted under a dissecting microscope (Osborne et al. 1985). Calvert (1987) describes a flotation method for extracting larvae from soil that utilizes reduced air pressure and magnesium sulphate to separate the larvae from organic debris.

Management

Current control practices for fungus gnats rely heavily on chemical applications (Hamlen and Mead 1979, Lindquist et al. 1985). In addition to their potential role in the dissemination of plant pathogens, fungus gnats may become an even more serious pest when insecticide resistance develops (Lindquist et al. 1985, Nedstam and Burman 1990).

Control practices have been suggested for fungus gnats that offer alternatives to the exclusive use of synthetic chemical insecticides. Such control methods include screening vents and doorways to impede the entrance of fungus gnats and placement of an attractant light near a sticky surface to trap adults (Thomas 1931). A layer of sand also can be added over the top of potting media to inhibit infestation by fungus gnats (Hungerford 1916).

Several biological control strategies also have been developed for use against fungus gnats. Application of the entomopathogenic bacterium, *Bacillus thuringiensis* Berliner var. *israelensis,* reduced surviving fungus gnats by 92% in comparison with water only control treatments (Osborne et al. 1985). Soil-dwelling predatory mites significantly reduced populations of fungus gnats when applied to cucumbers grown hydroponically (Gillespie and Quiring 1990). Additional studies of this mitc, *Hypoaspis* (*Stratiolaelaps*) *miles* (Berlese), have determined that all larval stages of *B. paupera* Toum are attacked, but the smaller larvae or early instars are more readily consumed, whereas, the eggs and pupae are generally untouched (Wright and Chambers 1994).

Tetradonematid nematodes that parasitize fungus gnats have been studied for use in biological control of these insects. *Tetradonema plicans* Cobb was isolated from *B. coprophila* by Hungerford (1919) who studied the general life history and distribution of this parasite. Hudson (1974) later isolated *T. plicans* from *B. paupera* and tested it as a biological control agent against this fungus gnat in British greenhouses. She found the nematode to be easily mass-reared, possessed a high reproductive rate, and could be stored as eggs for up to one year. Although *T. plicans* possessed these attributes and was highly host specific for *B. paupera*, this nematode was ineffective as a biological control agent because it was not highly lethal. Conversely, *Tripius sciaridae* (Bovien), an aphelenchoidid nematode parasite of fungus gnats, had previously been shown to quickly reduce sciarid populations in greenhouses, but lacked any stage that survived storage making it unsuitable for mass production (Poinar 1965).

Steinernematid nematodes also have been examined as potential biological control agents for fungus gnats. Bovien (1937), in his seminal work on *Neoaplectana bibionis* (Bovien) (syn. *Steinernema feltiae* [Filipjev] (Poinar 1990]), explored infection of nematoceran flies by steinermatid nematodes. These nematodes have been used to reduce fungus gnat numbers in glasshouse production. Over a 3-year period, the number of Swedish pot plant producers

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using *N. carpocapsae* (syn. *S. carpocapsae* [Weiser]) (Umeå-Musca strain to control fungus gnat larvae increased to 20% (Nedstam and Burman 1990). Linquist and Piatkowski (1993) tested two isolates each of *S. feltiae* and *S. carpocapsae* against *B. coprophila* in both Petri dish and greenhouse experiments. Although much variation was observed in adult emergence, reductions of fungus gnats were observed with three of the four isolates tested. In a subsequent study, the predatory mite *H. miles* was more effective against fungus gnats than either *S. feltiae* Otio or *S. carpocapsae* Umeå (Linquist et al. 1994). Harris et al. (1995) found *S. feltiae* SN strain to infect a significantly greater percentage of exposed *B. coprophila* than *S. feltiae* UK strain, *S. carpocapsae* All strain, or *H. bacteriophora* NC strain, although each nematode species and strain successfully infected this insect. The second and fourth larval instars were determined to be more susceptible to infection by *S. feltiae* than the pupal stage; however, pupae were infected by each nematode tested, although not at a significantly high level. The UK strain of *S. feltiae* also has been used successfully to control *B. paupera* in British greenhouses (Gouge and Hague 1994).

Hymenopterous parasites of sciarids include several species in the family Diapriidae (Nixon 1957, Hellén 1964). A recent study by Hellqvist (1994) indicates an unidentified species in the genus *Synacra* (Diapriidae, subfam. Belytinae) could be a useful biological control agent of *B. paupera* in Swedish greenhouses. This hymenopterous prasite successfully develops in each of the last three larval instars of *B. paupera*. A parasitized larva lives until pupation at which time it is killed and the wasp itself then pupates. The wasp has a potential maximum rate of population increase that is higher than that of *B. paupera* at 23°C, indicating the wasp to be an efficient parasite. However, larvae may cause additional plant damage during the interval between parasitization by this wasp and death, which Hellqvist points out as a disadvantage of using *Synacra* sp. to control fungus gnats in comparison with entomopathogenic nematodes.

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